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ARBOREAL SPIDERS (ARANEAE) ON BALSAM FIR AND SPRUCES IN EAST-CENTRAL MAINE

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ABSTRACT

Spiders of 11 families, 22 genera, and at least 33 species were collected from crown foliage samples of *Abies balsamea* (L.) Mill., *Picea rubens* Sarg., and *Picea glauca* (Moench) Voss in east-central Maine. For both study years (1985, 1986), spider species composition varied by foraging strategy (web spinner, hunter) and among 10 study sites. Numbers, life stages, and sex ratios of spiders also differed between study years. Spider densities per m^2 of foliage area generally were greater ($P \leqq 0.05$) on spruces ($\bar{X} = 16.3 \pm 1.1$) than on fir ($\bar{X} = 10.9 \pm 1.0$). Estimates of absolute populations of arboreal spiders ranged from 35,139 to 323,080/ha; of spruce budworm from 271,401 to 6,122,919/ha. Spider-budworm densities/ha covaried significantly ($P \leqq 0.001$) each year ($r = 0.84$, 1985; $r = 0.71$, 1986). None of the measured forest-stand parameters (basal area, tree species percentage) were reliable predictors of spider populations/ha.

INTRODUCTION

Recent devastating outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), have renewed interest in determining potential natural enemies of this defoliator of northeastern spruce-fir forests. Because of their ubiquitous occurrence, relative abundance, and predatory habits, spiders are considered important predators of the spruce budworm (Morris 1963; Jennings and Crawford 1985). Watt (1963) estimated that only 0.49 larvae/m^2 of tree foliage would have to be eaten by predators, including spiders, to account for a decrease in population survival rate of the spruce budworm.

A necessary first step for determining potential natural enemies of any pest is identification of the associated fauna. Some information is available about spiders of northeastern spruce-fir forests; however, most studies concern the terricolous fauna (Freitag et al. 1969; Carter and Brown 1973; Varty and Carter 1974; Jennings et al. 1988; Hilburn and Jennings 1988). Few previous studies have dealt with the arboreal spiders found on foliage of spruces (*Picea* spp.) and firs (*Abies* spp.); only one study (Jennings and Collins 1987) was completed in Maine.

During recent investigations of microsporidia-infected budworms, arboreal spider and spruce budworm populations were assessed on balsam fir, *Abies balsamea* (L.) Mill., red spruce, *Picea rubens* Sarg., and white spruce, *Picea glauca* (Moench) Voss trees in east-central Maine. This paper describes the arboreal-spider fauna associated with these coniferous tree species, compares spider-spruce budworm population densities among study sites and between host-tree species, estimates absolute population densities of spiders and budworms per hectare, and explores possible relationships among spiders, budworms, and forest-stand parameters.

METHODS

Study areas.—Six forest stands were investigated in 1985; four were investigated in 1986. All study sites were in east-central Maine (Fig. 1), and were in open, fir-spruce stands that had moderate to heavy infestations of spruce budworm. Site locations, abbreviations, and sampling years were:

Big Lake (BL)-T27 ED, Washington County; 1985.
Deer Lake (DL-'85)-T34 MD, east, Hancock County; 1985.
Deer Lake (DL-'86)-T34 MD, south, Hancock County; 1986.
Eastern Road (ER)-Upper Molunkus Twp., Aroostook County; 1985.
Machias River (MR)-T31 MD, Washington County; 1986.
Myra (MY-'85)-T32 MD, Hancock County; 1985.
Myra (MY-'86)-T32 MD, east, Hancock County; 1986.
Old Stream (OS)-T31 MD, Washington County; 1986.
Raven (RA)-Macwahoc Plt., Aroostook County; 1985.
River Road (RR)-Mattawamkeag Twp., Penobscot County; 1985.

At each study location, linear transects (0.5 to 1 km) were established along old logging roads or forest trails. We used a variable-size plot design to facilitate tree selection. Branch samples were obtained with a long, extendable pole pruner. Ten or 20 dominant/codominant trees of each category (balsam fir-red spruce; balsam fir-white spruce; balsam fir) were selected, flagged, and numbered for consecutive sampling on a weekly basis.

Stand measurements.—The variable-plot sample method (Wenger 1984) was used to determine basal areas (m^2/ha) of balsam fir, spruces (both red and white), northern white-cedar, *Thuja occidentalis* L., eastern white pine, *Pinus strobus* L., eastern hemlock, *Tsuga canadensis* (L.) Carr., and hardwoods (mostly *Acer* spp. and *Betula* spp.). At each study site (except DL-'85), ten 10-factor prism plots were established and all trees $\geqq$ 2.54 cm tallied by species or species group (e.g., spruces, hardwoods). Only four prism plots were taken at DL-'85.

Branch samples.—Trees were sampled at about weekly intervals both study years. In 1985, sampling began 20 May and ended 12 July; in 1986, sampling began 10 June and ended 2 July. Each year, the duration of the sampling period corresponded with the early larval (L_3-L_4) through pupal stages of the spruce budworm. This allowed determination of predator-prey densities when budworm larvae and pupae are susceptible to predation (Morris 1963).

At each sampling, one 45-cm branch was pruned from the upper crown half of each sample tree. Sectional, aluminum pole pruners equipped with a cloth-basket attachment below the pruner head were used to cut and lower branches to the

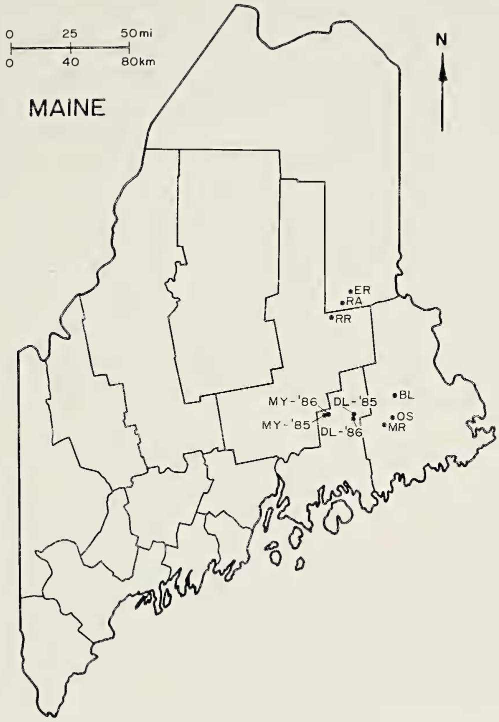

Fig. 1.—Study-site locations in east-central Maine, 1985, 1986. (See text for abbreviations).

ground. Jennings and Collins (1987) found that more spiders were collected when pole pruners were equipped with a catchment basket than with a clamping device (Stein 1969). At ground level, the severed branch and any dislodged arthropods were removed from the basket and placed in a labeled plastic bag for transport to the laboratory.

In the laboratory, trained technicians clipped branches into small lengths (8 to 10 cm) and closely searched all foliage for spruce budworms and spiders. All collected spiders were stored in 2-dram vials containing 75% ethanol.

Spider identifications.—Only sexually mature spiders were identified to species, following identification keys and species descriptions of Kaston (1981) and other consulted sources. Juveniles, including penultimate stages, were identified to generic level, and juveniles of two recognizable species groups (*Philodromus aureolus* and *P. rufus*) were assigned to either group based on color patterns of legs, carapace, and abdomen (Dondale and Redner 1978). Representative specimens of all identified species are deposited in the arachnid collection, U.S. National Museum of Natural History, Washington, DC.

Data analyses.—Branch surface areas were calculated by the formula: $A = (L\ X\ W)/2$, where L is branch length and W is maximum width (Sanders 1980). Population densities were expressed as spiders or spruce budworms/m^2 of branch foliage area. To estimate absolute populations, we converted spider-budworm densities/m^2 of foliage area to densities/ha by the method of Morris (1955). Populations were computed as:

$$\text{spiders/ha} = [\bar{X}\ \text{spiders/m}^2\ \text{of fir foliage} \cdot \sum_{F=1}^{N} \text{BSA}_F +$$

$$\bar{X} \text{ spiders/m}^2 \text{ of spruce foliage } \cdot \sum_{Sp=1}^{N} \text{BSA}_{Sp}], \text{ where}$$

$$\sum_{F=1}^{N} \text{BSA}_F = \text{sum of branch surface areas of } N \text{ fir trees/ha;}$$

$$\sum_{Sp=1}^{N} \text{BSA}_{Sp} = \text{sum of branch surface areas of } N \text{ spruce trees/ha.}$$

The following equations were used to calculate branch surface area per tree based on diameter at breast height (dbh):

$$\text{BSA}_F = -6.93 + 3.43 \text{ dbh}_{\text{cm}}, \text{ after Morris (1955)}$$
$$\text{BSA}_{Sp} = 2.64 + 3.34 \text{ dbh}_{\text{cm}}, \text{ after Dimond (unpubl.)}$$

Nonparametric procedures (Sokal and Rohlf 1981) were used for most statistical tests at $P = 0.05$. The Kruskal-Wallis Test (SAS Institute 1985) was used to compare spider-budworm densities among study sites and between tree species. Pearson correlation coefficient was used to test the interdependence of spider-budworm densities. Regression analyses were used to explore possible relationships between spider populations and measured stand parameters.

RESULTS

Forest stands.—Percentage composition of tree species by basal area (m^2/ha) indicated that most study sites had softwood components of balsam fir and spruces (mostly red spruce) (Table 1), with occasional eastern white pine, eastern hemlock, and northern white-cedar. With few exceptions, hardwoods accounted for $< 30\%$ of total basal area. Deer Lake (DL-'85) had a relatively high percentage of eastern hemlock; Myra (MY-'86) and Raven (RA) had high percentages of balsam fir.

Mean basal areas of fir and spruces generally were < 10 m^2/ha (Table 2), characteristic of open-grown stands. Mean tree diameters of firs ranged from 9.1 ± 3.9 cm to 17.5 ± 2.2 cm; mean diameters of spruces ranged from 10.7 ± 0.5 cm to 29.6 ± 2.3 cm. Tree heights of dominant/codominant sample trees were 10 to 15 m.

Spider taxa.—Spiders of 11 families, 22 genera, and at least 33 species were collected from arboreal habitats of spruce-fir forests in east-central Maine (Table 3). Fewer families, genera, and species were collected in 1986 than in 1985, but not unexpectedly because only balsam fir was sampled in 1986, and the sampling period was shorter. For both study years, species composition of spiders differed by foraging strategy; species of web spinners were slightly more prevalent in branch samples (56.2% of total species, 1985; 58.8% of total species, 1986) than species of hunters (43.8%, 1985; 41.2%, 1986).

Species per family ranged from one (Linyphiidae, Oxyopidae) to six (Erigonidae). In 1985, equal numbers of species (25) were collected from foliage

Table 1.—Percentage species composition of forest stands investigated for spiders and spruce budworms, east-central Maine, 1985-86.

Site	Fir	Spruces	Pine	Hemlock	Cedar	Hardwoods
1985 Study Sites						
BL	27.4	15.9	15.0		29.2	12.4
DL-'85	11.1	27.8	9.3	50.0		1.8
ER	4.3	20.5		39.3	25.6	10.2
MY-'85	40.0	21.1	2.2		1.1	35.6
RA	53.7	3.7	2.2	3.0		37.3
RR	33.6	10.9		29.1	0.9	25.5
1986 Study Sites						
DL-'86	44.4	41.6				13.9
MR	35.3	22.2	3.0	13.1	7.1	19.2
MY-'86	90.9	4.6	2.3			2.3
OS	45.6	14.7	7.4		4.4	27.9

samples of balsam fir and red spruce; only 12 species were collected from foliage of white spruce. In 1986, 17 species were collected from balsam fir foliage, the only tree species sampled that year. Because sampling intensities differed between years, adult spiders of 15 species were collected in 1985 but not in 1986; whereas, adults of only two species, *Mangora placida* (Hentz) and *Eris militaris* (Hentz), were collected in 1986 but not in 1985. Adults of 14 species were collected in both years.

Composition of spider species differed among study sites each year, no doubt because the sites were not identical (Tables 1 and 2) both years. In 1985, adult species per site ranged from 8 to 20 ($\bar{X}$ = 14.3); in 1986, from 6 to 14 ($\bar{X}$ = 10.0). Species common to all six sites sampled in 1985 were *Dictyna brevitarsus* Emerton, *Theridion murarium* Emerton, *Pityohyphantes costatus* (Hentz), *Grammonota angusta* Dondale, and *Metaphidippus flaviceps* Kaston. Both *Grammonota pictilis* (O.P.-Cambridge) and *Philodromus exilis* Banks were found on five study sites in 1985. Only one species, *Metaphidippus flaviceps*, was common to all four sites sampled in 1986; however, *Theridion differens* Emerton, *Pityohyphantes costatus*, and *Grammonota angusta* were each found on three sites.

Table 2.—Mean (±SE) basal areas of balsam fir and spruces in forest stands investigated for spiders and spruce budworms, east-central Maine, 1985-86. Mean (±SE) basal area (m^2/ha).

Site	Fir	Spruces
1985 Study Sites		
BL	7.1 (2.4)	4.1 (2.2)
DL-'85	3.4 (2.0)	8.6 (2.0)
ER	1.2 (0.6)	5.5 (1.0)
MY-'85	8.3 (3.1)	4.4 (1.0)
RA	16.5 (2.3)	1.2 (0.5)
RR	8.5 (1.7)	2.8 (1.0)
1986 Study Sites		
DL-'86	3.7 (0.5)	3.4 (0.8)
MR	8.0 (1.0)	5.0 (1.4)
MY-'86	9.2 (1.3)	0.5 (0.3)
OS	7.1 (0.9)	2.3 (1.0)

Table 3.—Arboreal spiders on foliage of *Abies balsamea, Picea rubens*, and *Picea glauca*, east-central Maine, 1985-86.

FAMILY	BALSAM FIR			SPRUCES		
Species	♂	♀	juv.	♂	♀	juv.
	WEB SPINNERS					
DICTYNIDAE						
Dictyna brevitarsus Emerton	6	13		5	15	
Dictyna phylax Gertsch & Ivie	2	4			6	
Dictyna sp.			24			39
THERIDIIDAE						
Theridion differens Emerton		1				
Theridion montanum Emerton		3			4	
Theridion murarium Emerton	5	7		4	10	
Theridion sp.			37			39
LINYPHIIDAE						
Pityohyphantes costatus (Hentz)	1	10		3	8	
Pityohyphantes sp.						7
ERIGONIDAE						
Ceraticelus atriceps (O.P.-Cambridge)		1				
Ceraticelus sp.						1
Dismodicus bifrons decemoculatus (Emerton)					1	
Grammonota angusta Dondale	10	56		17	59	
Grammonota pictilis (O.P.-Cambridge)	4	10		4	11	
Grammonota sp.						5
Pocadicnemis americana Millidge				1	1	
Walckenaeria lepida (Kulczynski)		1				
ARANEIDAE						
Araniella displicata (Hentz)	3	9			5	
Araniella sp.			1			3
Araneus sp. (nr. *saevus*)			1			1
Araneus sp.			1			
Cyclosa conica (Pallas)					1	
Cyclosa sp.						1
Mangora placida (Hentz)		3				
Neoscona arabesca (Walckenaer)				1		
Neoscona sp.			4			2
TETRAGNATHIDAE						
Tetragnatha versicolor Walckenaer		1		2		
Tetragnatha viridis Walckenaer	1					1
Tetragnatha sp.			2			4
Subtotals	32	119	70	37	121	103
	HUNTERS					
OXYOPIDAE						
Oxyopes sp.			1			
CLUBIONIDAE						
Clubiona canadensis Emerton		2			1	
Clubiona trivialis C. L. Koch	1	1				
Clubiona sp.			4			11
PHILODROMIDAE						
Philodromus exilis Banks	1	6		2	6	
Philodromus pernix Blackwall		1			3	
Philodromus placidus Banks		5			6	
Philodromus praelustris Keyserling				1		
Philodromus rufus vibrans Dondale		1				
Philodromus sp. (*aureolus* grp.)			3			1

Philodromus sp. (*rufus* grp.)			14			26
Philodromus sp.			15			33
THOMISIDAE						
Misumena vatia (Clerck)	1	1				
Misumena sp.						1
Xysticus punctatus Keyserling		4		2	1	
Xysticus sp.			19			40
SALTICIDAE						
Eris militaris (Hentz)	1	1				
Eris sp.			1			
Metaphidippus flaviceps Kaston	6	23		6	13	
Metaphidippus protervus (Walckenaer)				1		
Metaphidippus sp.			47			64
Salticus scenicus (L.)		1				
Subtotals	10	46	104	12	30	176
TOTALS	42	165	174	49	151	279

Spider numbers, life stages, sex ratios.—Over half (62.6%) of the total collected spiders (n = 765) in 1985 were from spruces. This high percentage was unexpected because of the distribution of branch samples among tree species in 1985, i.e., balsam fir (n = 60), red spruce (n = 50), and white spruce (n = 10). In 1986, all of the collected spiders (n = 95) were from balsam fir trees (n = 80).

In 1985, most collected spiders were juveniles (53.6%), followed by females (35.7%), and males (10.7%). In 1986, both juveniles and females were equally abundant (45.3% each) among collections, with fewer males (9.5%). Sex ratios of males to females were 1:3.3 in 1985 and 1:4.8 in 1986.

Spider densities.—For both study years, spider populations/m^2 of foliage area varied among study sites (Tables 4 and 5, column $\bar{X}$'s). In 1985, most sites had comparable means of 10 to 14 spiders/m^2 of balsam fir foliage and 19 to 20 spiders/m^2 of spruce foliage. In 1986, most sites had means of 7 to 14 spiders/m^2 of balsam fir foliage; spruce was not sampled that year. For unknown reasons, some sites had significantly fewer spiders (balsam fir-RA, DL-'86; spruces-ER, RA) than other sites.

Spider densities/m^2 of foliage generally were greater on spruces than on balsam fir (Table 4, row $\bar{X}$'s); these differences were significantly greater ($P \geqq 0.05$) on three of the study sites and over all sites in 1985. However, guild densities by foraging strategy (web spinner, hunter) were not significantly different ($P \geqq 0.05$) among tree species in 1985.

Budworm densities.—Populations of spruce budworm larvae and pupae/m^2 of foliage also varied among study sites both years (Tables 4 and 5, column $\bar{X}$'s). In 1985, mean densities were about equal between host tree species for most sites and over all sites. In 1986, most study sites had mean densities > 200 budworms/m^2 of balsam fir foliage; all sites $\bar{X}$ = 224.4 (± 10.4).

Absolute populations.—Estimates of arboreal spiders/ha ranged from 80,745 (± 17,643) to 323,080 (± 114,839) in 1985 [$\bar{X}$ = 192,073 (± 28,171)]; from 35,139 (± 5,338) to 287,024 (± 40,853) [$\bar{X}$ = 175,047 (± 20,287)] in 1986. Some of the observed variation among sites may be attributed to differences in percentage species composition of balsam fir and spruces (Table 1); however, spider densities/ha were weakly correlated with percentage fir (r = −0.08, 1985; r = 0.03, 1986), but more closely with percentage spruce (r = 0.30, 1985). Differences in percentages of balsam fir and spruces profoundly affected estimates of spiders/ha

Table 4.—Densities of spiders and spruce budworms/m^2 of foliage, balsam fir, red and white spruces, east-central Maine, 1985. *=White spruce sampled on MY-'85; red spruce sampled on all other sites. Column means (ab) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$. Row means (xy) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$.

	SPIDERS $\bar{X}$(± SE)/m^2		SPRUCE BUDWORMS $\bar{X}$(±SE)/m^2	
1985 SITES	Balsam fir	Spruces*	Balsam fir	Spruces*
BL	13.9ax (2.5)	20.2ay (2.7)	146.1bx (17.2)	99.4cy (11.5)
DL-'85	10.6ax (1.8)	20.4ay (3.2)	167.7bx (22.6)	179.4bx (28.0)
ER	10.5ax (3.8)	9.6bx (1.9)	54.8cx (11.9)	25.8dx (4.2)
MY-'85	12.7ax (2.4)	19.0ay (2.6)	212.6ax (21.9)	217.6ax (21.5)
RA	3.3bx (0.8)	8.4bx (1.8)	35.2cx (4.5)	34.3dx (6.3)
RR	14.3ax (2.4)	18.9ax (2.9)	145.6bx (17.5)	130.7bcx (14.6)
ALL	10.9x (1.0)	16.3y (1.1)	129.9x (7.8)	117.8x (7.9)

between tree species on the same site. For example, although spiders/m^2 of foliage were not significantly different between sampled tree species for study site ER in 1985 (Table 4), significantly more ($P \leqq 0.03$) spiders/ha were estimated to occur on spruces than on balsam fir, largely due to the preponderance of spruces ($5X >$ fir) on this site. The same pattern of influence also was evident for balsam fir; however, when host-tree differences were $\leqq 2X$, then spider densities/ha tended to equalize between tree species.

Estimates of absolute populations of spruce budworms/ha ranged from 271,401 (± 67,590) to 3,076,290 (± 928,941) in 1985 [$\bar{X}$ = 1,821,159 (± 273,181)]; from 2,465,473 (± 347,069) to 6,122,919 (± 1,091,369) in 1986 [$\bar{X}$ = 4,258,870 (± 422,723)].

Spider-budworm relationships.—Correlation analyses indicated positive significant associations between spider and budworm densities/ha each study year (Figs. 2 and 3). Spider and budworm densities covaried slightly more together in 1985 ($r = 0.84$, $P \leqq 0.001$) than in 1986 ($r = 0.71$, $P \leqq 0.001$), which might be attributed to population estimates derived from only one tree species in 1986. The scattered data points at relatively high spider-budworm densities (i.e., ≧ 400,000 spiders, ≧ 4.5 million budworms) indicated greater variation above these densities in 1985 (Fig. 2) than in 1986 (Fig. 3).

Spider/forest stands.—Regression analyses indicated that none of the measured forest-stand parameters were reliable predictors of spider populations/ha (Table 6). For unknown reasons, total basal area, fir basal area, and percent spruce were better indicators (i.e., higher r^2 values) of spider populations in 1986 than in 1985.

Table 5.—Densities of spiders and spruce budworms/m^2 foliage, balsam fir, east-central Maine, 1986. Column means (ab) followed by the same letter are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$.

1986 SITES	SPIDERS $\bar{X}$(±SE)/m^2	SPRUCE BUDWORMS $\bar{X}$(±SE)/m^2
DL-86	3.2b (1.0)	289.9a (20.7)
MR	9.4a (2.2)	118.6b (11.5)
MY-'86	7.0a (1.6)	235.2a (17.5)
OS	13.9a (2.4)	255.8a (24.6)
ALL	8.5 (1.0)	224.4 (10.4)

Fig. 2.—Association of spider-budworm densities per hectare, six study sites, east-central Maine, 1985. (Pearson Correlation Coefficient, r = 0.84, $P \leqq 0.001$). Small, medium, and large circles represent one, two, and three observations, respectively.

DISCUSSION

Spider taxa.—Many of the species of spiders we collected on foliage of balsam fir, red and white spruces in east-central Maine have been taken on balsam fir in New Brunswick (Loughton et al. 1963; Renault 1968) and on red spruce in northern Maine (Jennings and Collins 1987). Species not previously recorded from arboreal habitats of Maine's spruce-fir forests include *Pocadicnemis americana* Millidge, *Walckenaeria lepida* (Kulczynski), *Tetragnatha viridis* Walckenaer, *Philodromus praelustris* Keyserling, *Eris militaris* (Hentz), and *Metaphidippus flaviceps* Kaston.

Based on frequency of collection (this study and Loughton et al. 1963; Renault 1968; Renault and Miller 1972; Jennings and Collins 1987), we consider the following species as typical arboreal spiders of northeastern spruce-fir forests: *Dictyna brevitarsus* Emerton, *D. phylax* Gertsch & Ivie, *Theridion montanum* Emerton, *T. murarium* Emerton, *Pityohyphantes costatus* (Hentz), *Ceraticelus atriceps* (O.P.-Cambridge), *Grammonota angusta* Dondale, *Araniella displicata* (Hentz), *Clubiona canadensis* Emerton, *C. trivialis* C. L. Koch, *Philodromus exilis* Banks, *P. placidus* Banks, and *Xysticus punctatus* Keyserling.

Our observed differences in composition of spider species by foraging strategy (web spinners, 55%; hunters, 45%) generally agree with earlier studies. Jennings and Collins (1987) collected more species of web spinners (54%) than hunters (46%) from red spruce foliage in northern Maine (n = 21 species). Likewise, Jennings and Hilburn (1988) captured more species of web spinners (56%) than hunters (44%) in Malaise traps operated in spruce-fir forests of west-central Maine (n = 25 species). Even greater percentages of web spinners (67%) than hunters (33%) were reported associated with balsam fir foliage in New Brunswick, where n = 54 species (Loughton et al. 1963). We conclude that the web-spinner guild comprises a major species component of the arboreal spider fauna associated with northeastern spruce-fir forests.

The observed dissimilarities in composition of spider species among study sites may be within the realm of expected variation for northeastern spruce-fir forests.

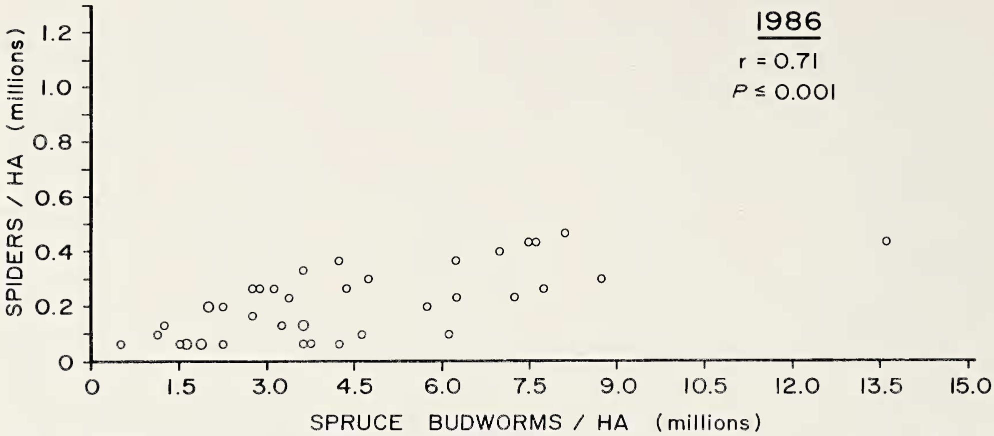

Fig. 3.—Association of spider-budworm densities/ha, four study sites, east-central Maine, 1986. (Pearson Correlation Coefficient, $r = 0.71$, $P \leqq 0.001$). Small, medium, and large circles represent one, two, and three observations, respectively.

Renault and Miller (1972:1045-46) noted "a remarkable constancy in the species composition in any one location," but "a marked dissimilarity in the species composition in different areas," all classed as fir-spruce biotype. Until additional studies are completed, the overall species composition of arboreal spruce-fir spiders remains undefined except for localized areas. No doubt, additional species will be added to the known fauna by the use of other sampling methods (e.g., whole-tree counts), extension of sampling periods, and increased sample sizes.

Spider numbers, life stages, sex ratios.—Some of the observed differences in spider numbers, life stages, and sex ratios can be attributed to reproductive cycles of individual species and production of young spiderlings during midsummer. At least five of the species found during this study, *Theridion murarium* Emerton, *Araniella displicata* (Hentz), *Misumena vatia* (Clerck), *Xysticus punctatus* Keyserling, and *Philodromus placidus*, have biennial life histories (Dondale 1961, 1977). Juveniles of *Theridion, Xysticus*, and *Philodromus* commonly were collected among branch samples, especially in 1985, and probably represented immature stages of biennial species.

The biased sex ratio in favor of females was not unexpected because female spiders generally live longer than males (Gertsch 1979), and males generally are more vagrant and hence less likely to be sampled than females. However, we are unable to explain why female spiders were slightly more prevalent among collections in 1986 (45.3%) than in 1985 (35.7%). Sample size (i.e., 878 branches in 1985 vs. only 298 branches in 1986) and sampling-time differences between years may have been contributing factors.

Spider densities.—The spider densities/m^2 of foliage that we observed in east-central Maine generally are greater than those previously reported elsewhere. Morris (1963) noted densities of 2.65 spiders/10 ft^2 (2.85/m^2) of balsam fir foliage in June and 2.34 spiders/10 ft^2 (2.52/m^2) in July, on the Green River Watershed, New Brunswick. For two plots on the same watershed and sampling dates comparable to our Maine study (22 May to 12 July), Loughton et al. (1963) reported densities ranging from 0.6 spiders/10 ft^2 (0.6/m^2) to 18.9 spiders/10 ft^2 (20.3/m^2) of balsam fir foliage. We calculated mean densities for these same plots and sampling periods as: K2 = 9.5 spiders/m^2 (1957), 7.9 spiders/m^2 (1958); G16 =

Table 6.—Coefficients of determination (r^2) for predicting spider populations/ha based on forest stand parameters.

	1985		1986	
STAND PARAMETER	r^2	P	r^2	P
Total basal area	0.06	0.65	0.31	0.44
Fir basal area	0.03	0.73	0.48	0.31
Spruce basal area	0.08	0.59	0.04	0.81
Percent fir	0.01	0.88	0.00	0.97
Percent spruce	0.09	0.56	0.56	0.25

7.9 spiders/m^2 (1957), 5.6 spiders/m^2 (1958). Renault and Miller (1972) noted a yearly constancy of about 8.2 spiders/m^2 of balsam fir foliage for a 9-year period (1962-70), on the Green River Watershed, New Brunswick.

For spiders on spruces, Morris (1963) reported densities of 4.8 spiders/10 ft^2 (5.2/m^2) in June and 12.5 spiders/10 ft^2 (13.4/m^2) in July, Green River Watershed, New Brunswick. In northern Maine, Jennings and Collins (1987) observed densities ranging from 1.5 to 16.6 spiders/m^2 and a mean density of 7.1 spiders/m^2 of red spruce foliage sampled in late July. The overall mean density of 16.3 spiders/m^2 of spruce foliage in east-central Maine was substantially greater than expected based on previous studies.

Absolute populations.—Our estimates of absolute populations of arboreal spiders/ha generally were less than some earlier findings, i.e., Morris (1963) estimated 187,500 spiders/ha in New Brunswick; Haynes and Sisojevic (1966) estimated 312,500/ha in New Brunswick; Jennings and Collins (1987) estimated 645,853/ha in north-central Maine. We suspect that stand species composition and stand density are important determinants of absolute populations of arboreal spiders. For example, the sites investigated in east-central Maine were open grown, fir-spruce stands; whereas, those estimated to harbor 645,853 spiders/ha were dense, red spruce stands (Jennings and Collins 1987). No doubt our estimates and those earlier are conservative because not all represented tree species were sampled. Total absolute populations of spiders/ha are apt to be much higher when estimates include all tree species and all strata (arboreal, epigeal, terrestrial).

Spider-budworm relationships.—Based on the observed high correlations between spider and budworm densities, we suspect that spiders were responding to available prey (budworm) populations in east-central Maine. All life stages of the spruce budworm—eggs, larvae, pupae, and adults—are susceptible to spider predation, but the larvae are particularly vulnerable because of their relative abundance, size, and activity. Loughton et al. (1963) investigated spider predation on the spruce budworm in New Brunswick and concluded that: (1) erigonids are the most important predatory group because of their large numbers; (2) theridiids are the most effective predators, based on percentages showing positive feedings on budworm; and (3) salticids are important predators at all stages of budworm larval development, including the late instars. Predation on the large larvae is especially important because mortality during the late larval stage influences generation survival of the spruce budworm (Morris 1963). All three spider families (Erigonidae, Theridiidae, Salticidae) were common among branch samples from balsam fir and spruces in east-central Maine.

Spiders/forest stands.—Small sample sizes (n = 6 sites, 1985; n = 4 sites, 1986) may have contributed to the weak relationships between forest-stand parameters and estimates of spider populations/ha in east-central Maine. Because of greater spider densities and lower coefficients of variation on spruce, we predict that percentage spruce will be a more reliable indicator of absolute spider populations/ha than percentage fir. However, numerous other factors, such as canopy closure, crown class, and stand age, warrant investigation.

Jennings and Collins (1987) hypothesized that red spruce may harbor more spiders, both individuals and species, than balsam fir. Our results in east-central Maine partially support this hypothesis, i.e., overall, significantly more ($P \leqq 0.001$) spiders/m^2 of foliage were found on spruces (red, white) than on balsam fir. We also found equal numbers of spider species (25) despite unequal sample sizes in favor of balsam fir. We suspect that additional spider species may occur on each tree species and that spruces provide greater microhabitat space for web building and for foraging by hunting spiders. In Minnesota, Stratton et al. (1979) found that white spruce had more spider individuals and species than red pine, *Pinus resinosa* Ait., and northern white-cedar. They attributed the greater spider diversity on spruce to differences in plant physiognomy, i.e., structure of needles and branches.

Results of our study in east-central Maine indicate that: (1) host-tree species influences arboreal-spider density per m^2 of foliage area, (2) percentage composition of tree species in forest stands affects overall estimates of arboreal-spider populations/ha, and (3) estimates of spider-budworm (predator-prey) densities may be highly correlated. Additional studies are needed to define and evaluate other factors that possibly influence spider populations on northeastern conifers. If indeed spruce supports greater populations of spiders than fir, forest pest managers will have the option to manage forests to increase populations of potential predators of the spruce budworm. Such options offer alternatives to reliance solely on chemical insecticides.

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